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13. ABSTRACT *(Maximum 200 words)*

Copepods are small (1-10 mm) crustaceans that inhabit lakes and oceans. When a copepod moves through water or moves water around itself, it creates a fluid disturbance distinct from the ambient fluid motion. In this study of 'Fluid mechanoreception by marine copepods', we seek an understanding of how copepods decipher and recognize fluid signals created and transmitted within a 3-dimensional aquatic environment that is filled with small-scale turbulence.

We have documented the fluid mechanical signals that various copepods make (6). We have modeled mathematically the flow in the copepod feeding current (1) and quantified the effect of the feeding current on both entrained odors (2) and prey (3). We have shown that other copepods respond to the fluid mechanical signals within the feeding current by escaping (5) and by attacking the wake shed by prey-sized copepods as they escape (4). A map of the sensors along the paired antennules (7) reveals a well-designed system for measuring signal intensity and 3-dimensional location of small-scale fluid features of the aquatic environemnt at appropriate temporal and spatial scales.

[(#) refer to citations of articles resulting from this research, as described in section F. RESULTS.]

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The Research Foundation
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State University of New York at Stony Brook

August 30, 1996

Dr. Bernard J. Zahuranec
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Re: N00014-92-J-01690, Dr. Jeannette Yen

Dear Dr. Zahuranec:

Enclosed is the original and two copies of the final technical report for the above referenced award.

If you have any questions or require any additional information, please feel free to contact me at 516-632-9039.

Sincerely,

Kristina Clenaghan

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Sponsored Programs Coordinator

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Fluid mechanoreception by marine copepods

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Copepods roam a three dimensional aquatic environment and their sensors reflect this: setal hairs on their paired antennules, primary sensors, are oriented in three orthogonal planes to intercept fluid flow in these directions. Behavioral responses indicate that some copepods use these sensors for fluid mechanoreception to recognize hydrodynamic signals. This investigation focused on the ability of a carnivorous copepod to remotely detect fluid deformations produced by its mobile prey which permit early detection of prey by the predator. This involves target recognition, 3D spatial localization of hydrodynamically conspicuous prey, and an ability to distinguish relevant signals from the ambient fluid motion. We measured behavioral responses of the copepod to stimuli that have been designed to mimic disturbances generated by their prey. Through empirical observations permitting flow visualization, we have ascertained certain components of the velocity field prevailing in the ocean that can be detected by the copepod.

With present studies of small-scale biological-physical interactions in the plankton, we are characterizing the signals created by escaping prey, lunging predators, and attractive mates. We seek an understanding of how copepods decipher and recognize fluid signals created and transmitted within a 3-dimensional aquatic environment that is filled with small-scale turbulence. Small-scale turbulence creates noise that either can mask important signals or provide structures that guide them. These studies of remote sensory perception by 1-10 mm aquatic crustaceans revealed the importance of fluid dynamics at low Reynolds numbers on the transmission of signals (light, odors, fluid flow) through the water at small temporal and spatial scales in three dimensions and the behavioral recognition by plankton of these cues.

This research motivates:
1. Continued development of visual techniques to quantify hydrodynamic disturbances generated by aquatic plankters.
2. Continued development of behavioral and physiological assays to test hypotheses concerning the validity of the hydrodynamic disturbance as one signal among others, that conveys information between zooplankton.
3. Future work to include the hazards and benefits of turbulence to signal recognition by planktonic organisms.

Our analyses of the character (magnitude, extent, persistence), transmission, and reception of the water-borne signals using certain behavioral responses of zooplankton as a measure of perception permit a better understanding of how these small-scale interactions influence the large-scale patterns noted for zooplankton, such as seasonal population dynamics (prey-predator interactions) or patchiness (swarming).

Publications and manuscripts from this research:

1. Stein, M., A. Okubo, and J. Yen. accepted. A mathematical model of the copepod feeding current: A fluid dynamical approach. J. Plankton Res.: The copepod feeding current has been modeled with a solution of the full Navier-Stokes equations at low Reynolds numbers for an incompressible fluid. Solving the equation for a steady jet from a source of momentum, a similarity solution of the jet was found. The model qualitatively is consistent with experimental data. Modification of the model to suit different flow structures created by different animals is possible by varying the one free parameter, the strength of the flow. This parameter provides a simple criterion for comparing different copepods. This model can be used to test hypotheses of copepod mechanoreception and chemoreception. The model also provides closed form expressions for the fluid velocity and vorticity.

2. Moore, P.A., D.M. Fields, J. Yen. in prep. The fine-scale structure of chemical signals within the feeding current of a calanoid copepod: With empirical measurements of fluid flow and chemical signals, we have shown that odor patches will be stretched and sheared by the fluid forces within the copepod feeding current. We use flow visualization techniques together with a new technique in chemical detection technology (IVEC-5). These odor patches become much more transient, much less variable and, in some locations near the animal, much stronger in intensity.

3. Fields, D.M. and J. Yen. accepted. Gyrotaxis: Implications of copepod feeding currents on the spatial orientation of their prey. J. Plankton Res.:
An empirically-determined velocity field of the feeding current of a predatory copepod was separated into their x- and y-components to compute vorticity. The balance of rotation and advection within the copepod feeding current influences gyrotactic reorientation of the mobile prey, steering them to jump ahead into the central capture region.

4. Yen, J. and Fields D. M. 1994. Behavioral responses of *Euchaeta rimana* to controlled fluid mechanical stimuli. EOS 75: 184: We have succeeded in designing a mimic of the hydrodynamic disturbance made within the wake shed by an escaping copepod. Using this controlled fluid mechanical signal, we can, on cue, elicit various responses from the mechanoreceptive copepod *Euchaeta*. Three characteristic responses elicited include: an antennal flick, maxilliped extension, swimming leg extension. These responses are part of their behavioral repertoire which includes turns, captures, and escapes, respectively. One of the responses to the miniature water jet: the escape, has a very brief latency of 3 msec where the force of the escape is approximately 2 g for a 6 mg copepod (*Gaussia princeps*).

5. Fields, D.M. and J. Yen. 1995. The escape behavior of *Pleuromamma xiphias* from a quantifiable fluid mechanical disturbance. Mar. Freshw. Behav. Physiol.25: During an escape, the copepod *Pleuromamma xiphias* can accelerate at 9G. Comparisons of the response of 5 species of copepod show that copepods from noisy environments (coastal surface layers) require high shear (25-50/sec) to elicit the escape while copepods living in quiet regimes (deep open ocean) escape from lower shear (1-10/sec). This response pattern suggests that copepods can filter some ambient hydrodynamic noise, found as a prevailing feature of the constantly moving fluid medium.

6. Yen,.J. and J.R. Strickler. in press. Advertisement and concealment in the plankton: What makes a copepod hydrodynamically conspicuous? Invert. Biol.: Copepods are small (1--10 mm) crustaceans that inhabit lakes and oceans. Our focus is on *Euchaeta rimana*, a pelagic marine copepod. It roams a 3 dimensional ambit and its

antennulary setal sensors are oriented to detect water-borne signals in 3 dimensions. When the copepod moves through water or moves water around itself, it creates a fluid disturbance distinct from the ambient fluid motion. As it swims and hovers, the copepod's laminar feeding current takes the unstable nature of small-scale turbulence, organizes it, and makes the local domain a familiar territory within which signals can be specified in time and space. The streamlines betray both the 3 dimensional spatial location (x,y,z) as well as the time (t) separating a signal caught in the feeding current and the copepod receptor. This information gives the copepod early warning of the approach of a prey, predator, or mate. The copepod reduces the complexity of its environment by fixing information from a turbulent field into a simpler, more defined laminar field.

We quantitatively analysed small-scale fluid deformations created by copepods to document the strength of the signal. Physiological and behavioral tests confirm hypotheses that these disturbances are relevant signals transmitting information between zooplankters. These studies reveal that hydrodynamically conspicuous structures, such as feeding currents, wakes, and vibrations, elicit specific responses from copepods. Since fluid mechanical signals do elicit responses, copepods shape their fluid motion to advertise or to conceal their hydrodynamic presence. When swimming, a copepod barely leaves a trace in the water. The animal generates its flow, advances into the area from which the water is taken, covering up its tracks with the velocity gradient it creates around itself. When escaping, it sheds conspicuous vortices. Prey caught in a flow field, expose their location by hopping. These escape hops shed jet-like wakes that are detectable by mechanoreceptive copepods. Copepods recognize these structures and react with responses that are advantageous for their survival in the aquatic habitat.

7. Boxshall GA, Yen J, & Strickler JR 1997. Functional significance of the sexual dimorphism in the cephalic appendages of *Euchaeta rimana* Bradford. Bull. Mar. Sci. 60: Sexual dimorphism in antennulary setulation of *Euchaeta* reveals the functional importance of the 4-point setular array in providing sensors for prey detection. The antennule has a linear array of closely-spaced setae that fold distally. This improves the streamlined form when the antennules are swept down close to the body during escape leaps. This biosensor is well-designed to measure the signal intensity and 3D location of small-scale features of the aquatic environment at appropriate temporal and spatial scales.

8. Fields D. M. 1996. Interactions of marine copepods with a moving fluid environment. Ph.D. dissertation. State University of New York at Stony Brook. 403 p.

9. Fields, D. and J. Yen. 1993. Outer limits and inner structure: The 3-dimensional flow fields of *Pleuromamma xiphias*. Bulletin of Marine Research 53: 84-95.

10. Yen, J. and D. Fields. 1992. Escape responses of *Acartia hudsonica* nauplii from the flow field of *Temora longicornis*. Archiv für Hydrobiologie Beiheft 36: 123-134.

11. Schultze, P.C., J.R., Strickler, B.I Bergström, M.S. Berman, P. Donaghay, S. Gallager, J.F. Haney, B.R. Hargreave, U. Kils, G.-A. Paffenhöfer, S. Richman, H.A. Vanderploeg, W. Welsch, D. Wethey, J. Yen. 1992. Video-based instruments for *in situ* studies of zooplankton abundance, distribution, and behavior. Arch. Hydro. Beih. 36: 1-21.

12. Yen, J. and A. Okubo. in prep. Particle and prey detection by mechanoreceptive copepods: A mathematical analysis.